



Anais da Academia Brasileira de Ciências

ISSN: 0001-3765

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Academia Brasileira de Ciências
Brasil

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Anais da Academia Brasileira de Ciências, vol. 87, núm. 2, abril-junio, 2015, pp. 669-689

Academia Brasileira de Ciências

Rio de Janeiro, Brasil

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Comments on Triassic pterosaurs with discussion about ontogeny and description of new taxa

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Manuscript received on April 27, 2015, accepted for publication on May 13, 2015

ABSTRACT

Eudimorphodon ranzii was the first Triassic pterosaur to be described and several specimens have been referred to this taxon mainly based on the presence of multicuspid teeth. Since this dental feature has been observed in several other pterosaurs, the revision of some specimens assigned to *Eudimorphodon* shows that they represent new taxa as follows: *Arcticodactylus cromptonellus* (comb. nov.), *Austriadraco dallavecchiai* (gen. et sp. nov.) and *Bergamodactylus wildi* (gen. et sp. nov.). A preliminary analysis of pterosaur ontogeny resulted in the recognition of six distinct ontogenetic stages (OS1-6). According to this classification, the holotype of *Arcticodactylus cromptonellus* has reached OS2, and although being ontogenetically much younger than others, the conspicuous anatomical differences lead to its exclusion from *Eudimorphodon*. The holotypes of *Austriadraco dallavecchiai*, *Bergamodactylus wildi* and *Carniadactylus rosenfeldi* have reached at least OS5, which demonstrates that the anatomical differences among them cannot be explained by ontogeny. Moreover, *Bergamodactylus wildi* reaches about 60% of the maximized wingspan of *Carniadactylus rosenfeldi* and further concurs that these specimens collected in distinct Triassic Islands of Europe are not conspecific. The present study increases the diversity of Triassic flying reptiles and further pushes the origins of this clade back to at least the Middle Triassic.

Key words: Pterosauria, Ontogeny, *Eudimorphodon*, *Arcticodactylus*, *Austriadraco*, *Bergamodactylus*.

INTRODUCTION

The pterosaur record from Triassic deposits is rather limited (Barrett et al. 2008), although the number of new specimens has increased throughout the years (Dalla Vecchia 2014). Since the description of *Eudimorphodon ranzii* from the late Norian deposits of Italy (Zambelli 1973), more material has been found, for all in Europe (e.g., Wild 1978, Dalla Vecchia 2003a, b, 2014).

Being the first Triassic pterosaur named, *Eudimorphodon ranzii* shows a very distinctive dentition formed by several multicuspid teeth, a feature regarded as diagnostic of the genus (Wild 1978, Dalla Vecchia 2003a). Consequently, most specimens with similar dentition were either referred to *Eudimorphodon ranzii* (e.g., Wild 1978, 1994), including a partial skeleton recovered from the Seefeld Formation of Austria (Wellnhofer 2003), or to the genus as happened with '*Eudimorphodon*'

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rosenfeldi from the Dolomia di Forni Formation of Italy (Dalla Vecchia 1995) and '*Eudimorphodon*' *cromptonellus* from the Fleming Fjord Formation of Greenland (Jenkins et al. 2001).

In a cladistic analysis addressing the ingroup relationships of the Pterosauria, which included the main representatives of non-pterodactyloid and pterodactyloid taxa known at that time, Kellner (2001, 2003) pointed out that not all specimens referred to *Eudimorphodon ranzii* might belong to this species, which he restricted to the holotype (MCSNB 2888). Kellner (2003) also observed that the multicuspoid dentition was not exclusive of *Eudimorphodon*, being also present in at least some teeth of *Peteinosaurus zambellii*. This author further pointed out several anatomical differences between the Milano specimen (MPUM 6009) and the holotype of *Eudimorphodon ranzii* and argued that '*Eudimorphodon*' *rosenfeldi* should be classified in a new genus. This clearly indicated that *Eudimorphodon* has become a wastebasket for several pterosaur species.

Reviewing the record of Triassic flying reptiles, Dalla-Vecchia (2003b) retained the Milano specimen (MPUM 6009) in the genus *Eudimorphodon* but suggested that it might belong to a distinct species. Dalla Vecchia (2003b) also pointed out that the Austrian material regarded by Wellnhofer (2003) as *Eudimorphodon* cf. *Eudimorphodon ranzii* was not conspecific with *Eudimorphodon ranzii*. Lastly, this author mentioned that the synonymy of *Eudimorphodon cromptonellus* and *Eudimorphodon ranzii* could not be excluded. Later, Dalla Vecchia (2009) erected the genus *Carniadactylus* for '*Eudimorphodon*' *rosenfeldi* and referred the Milano specimen (MPUM 6009) to this species.

In the present paper I briefly review the species and some specimens assigned to *Eudimorphodon ranzii*. I show that '*Eudimorphodon*' *cromptonellus* lacks any synapomorphy of *Eudimorphodon* and reallocate this species into a new genus,

Arcticodactylus gen. nov. The same is true for the Austrian '*Eudimorphodon*' for which I propose a new genus and species, *Austriadraco dallavecchiai* gen. et sp. nov. I also question the assignment of the Milano specimen (MPUM 6009) to either, *Eudimorphodon ranzii* and *Carniadactylus rosenfeldi*, and argue that it represents a new campylognathoidid Triassic taxon, *Bergamodactylus wildi* gen. et sp. nov. Lastly, I provide some discussion about the problematic regarding pterosaur ontogeny, suggesting a preliminary classification that might help distinguish different ontogenetic stages within this clade of flying reptiles.

Anatomical abbreviations: ang - angular, aof - antorbital fenestra, art - articular, cor - coracoid, d - dentary, exmf - external mandibular fenestra, f - frontal, fe - femur, fo - foramen, fopn - foramen pneumaticum, hu - humerus, j - jugal, l - left, la - lacrimal, ltf - lower temporal fenestra, m - maxilla, maxws - maximized wingspan, mcIV - metacarpal IV, n - nasal, nar - external naris, or - orbit, p - parietal, ph1d4 - first phalanx of manual digit IV, ph2d4 - second phalanx of manual digit IV, ph3d4 - third phalanx of manual digit IV, pm - premaxilla, po - postorbital, q - quadrate, qj - quadratojugal, r - right, rapr - retroarticular process, ri - rib, san - surangular, sandp - surangular dorsal process, sca - scapula, sq - squamosal, st - sternum, ti - tibia, ul - ulna, utf - upper temporal fenestra.

Institutional abbreviations: BSP - Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Germany; MCSNB - Museo Civico di Scienze Naturali di Bergamo, Bergamo, Italy; MFSN - Museo Friulano di Storia Naturale, Udine, Italy; MGUH - Geological Museum of Copenhagen, University of Copenhagen, Denmark; MPUM - Museo di Paleontologia dell'Università di Milano, Milano, Italy; SMNS - Staatliches Museum für Naturkunde, Stuttgart, Germany.

The ZooBank Life Science Identifier (LSID) of this publication is: urn:lsid:zoobank.org:pub:A48E1B7C-1EEE-4AB2-A6BE-CC3D2DCCAEFF.

SYSTEMATIC PALEONTOLOGY

Pterosauria Kaup 1834

Family indet.

Arcticodactylus gen. nov.

ZooBank Life Science Identifier (LSID) -
urn:lsid:zoobank.org:act:72AE012A-018A-4B4B-
950F-3CCB4C1D2471

Etymology: In allusion to Arctic, the most northern region of the planet, and *dactylus*, from the Greek meaning finger, a common epithet for pterosaur species.

Type species: *Eudimorphodon cromptonellus* Jenkins, Shubin, Gatesy and Padian, 2001, by monotypy.

Diagnosis: as for the species.

Arcticodactylus cromptonellus comb. nov.

Eudimorphodon cromptonellus Jenkins, Shubin, Gatesy and Padian, 2001

Holotype: Incomplete skeleton housed in the Geological Museum of Copenhagen, University of Copenhagen, Denmark (MGUH VP 3393, Fig. 1, Tabs. I, II).

Locality and horizon: Southern flank of Macknight Bjerg, Jamerson Land, East Greenland; lower part of the Carlsberg Fjord beds of the Ørsted Dal Member of the Fleming Fjord Formation, Scoresby Lang Group, Late Triassic (?Norian - Rhaetian, Jenkins et al. 2001).

Revised diagnosis: This species shows the following autapomorphies: 11-12 maxillary multicuspid teeth; distal articulation surface of wing metacarpal IV bicondylar, femur only slightly smaller than tibia (fe/ti ~0.96); scapula much longer than coracoid (sca/cor ~ 1.93); humerus only slightly smaller than femur (hu/fe - 0.92) and ulna (hu/ul ~ 0.91); femur slightly larger than first wing phalanx (ph1d4/fe ~ 0.91); and elongated metatarsal III (mt3/ti 0.56).

It can be further separated from some other non-pterodactyloids by the lack of the fang-like teeth in the middle part of the lower jaw and the triangular shape of the deltopectoral crest of the humerus.

Remarks: The specimen MGUH VP 3393 consists of one of the smallest pterosaurs recovered so far, particularly from Triassic strata. Jenkins et al. (2001) erected a new species to this material referring it to the genus *Eudimorphodon* mainly due to the presence of multicuspid teeth. As Kellner (2003) pointed out, the presence of multicuspid teeth is not exclusive of *Eudimorphodon*, which has been emphasized in recent years due to new findings (e.g., see review in Dalla Vecchia 2014). Furthermore, the humerus of the Arctic species has a triangular deltopectoral crest that differs from the subrectangular condition observed in the Triassic campylognathoidids *Eudimorphodon ranzii*, *Carniadactylus* and *Bergamodactylus*.

Another bone of MGUH VP 3393 that shows a very distinct morphology is the quadrate (oddly about the same length of the bone identified as the coracoid). Jenkins et al. (2001) only mentioned that this bone has a bulbous articular condyle. In the illustration provided (Jenkins et al. 2001, fig. 2), the quadrate shaft is unusually broad, differing from all pterosaur quadrates known to me, yet showing a morphology very similar to some Triassic pterosaur coracoids (see Dalla Vecchia 2009, fig. 3). In addition, Jenkins et al. (2001, fig. 5) pointed out that the distal articulation of the wing metacarpal is formed by rounded condyles separated by a strong groove, calling it bicondylar. If these interpretations are correct, both the shapes of the quadrate and the wing metacarpal of this Arctic species are unique within Pterosauria and deserve further studies.

In the last review of *Eudimorphodon ranzii* (and other Triassic pterosaur material), Dalla Vecchia (2014) presented several features that diagnose this monotypic genus. Unfortunately, most of them cannot be evaluated in the Arctic species due to lack of preservation. The few characters that can be compared such as the presence of fang-like teeth in the middle portion of the dentition, teeth on the pterygoids and enamel of several teeth striated, are not present in MGUH VP 3393.

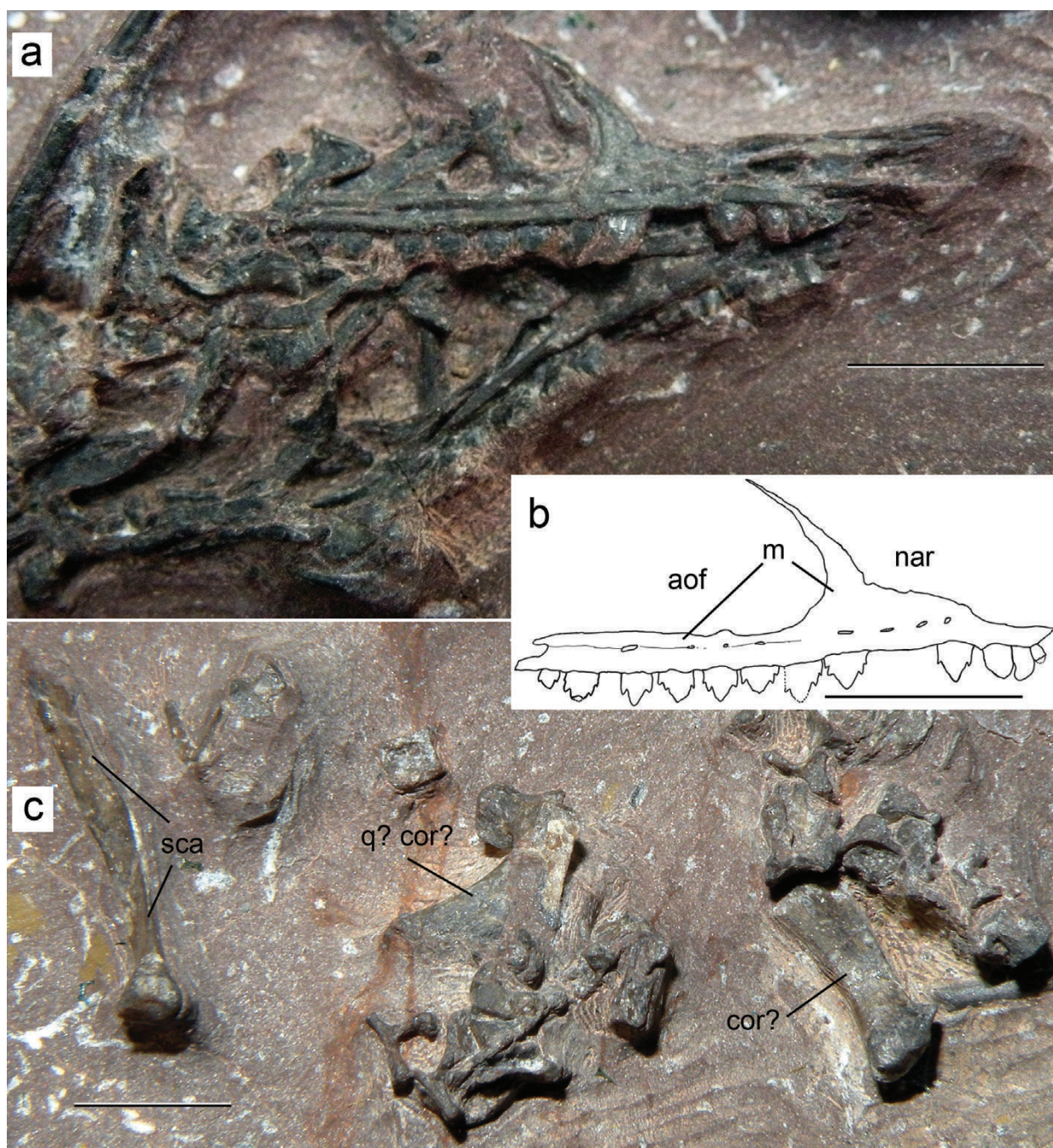


Fig. 1 - *Arcticodactylus cromptonellus* (MGUH VP 3393). (a) Preserved portion of the skull. (b) Reconstruction of the right maxilla. (c) Region showing the scapula and purported coracoid and quadrate. See text for abbreviations. Scale bar: 5 mm.

In addition, the proportions of several elements of '*Eudimorphodon*' *cromptonellus* are quite different from those of *Eudimorphodon ranzii* and several other Triassic taxa. These include a comparatively small humerus, ulna and first wing phalanx, and

an elongated metatarsal III, suggesting that this animal had short wings and large feet (Jenkins et al. 2001). MGUH VP 3393 also has fewer maxillary teeth than all other Triassic pterosaurs for which the dentition could be reconstructed. These

TABLE I

Measurements (in mm) of postcranial elements of some Triassic pterosaur species, based on published information or taken by the author (AWAK). Some lengths are estimated (~) and in one case the bone should be longer (+). Some published estimated lengths of very incomplete elements were not considered. See text for abbreviations.

Bones/Taxa	sca	cor	hu	ul	mcIV	ph1d4	ph2d4	ph3d4	fe	ti	Author
<i>Arcticodactylus</i> <i>cromptonellus</i> MGUH VP 3393	12.6	6.5+	18.2	20.1	8.4	~18	20.5	20.5~	19.7	~20.5	Jenkins et al. (2001)
<i>Austriadraco</i> <i>dallavecchiai</i> BSP 1994 I 51	~29.5	18.2	~39 (r) ~40 (l)	-	-	52.9	-	-	-	57.7	Wellnhofer (2003) / AWAK
<i>Eudimorphodon</i> <i>ranzii</i> MCSNB 2888	-	-	47	65	29	-	-	-	41	-	Wild (1978)
<i>Carniadactylus</i> <i>rosenfeldi</i> MFSN 1797	-	22.5	~42	~55	21	64.5	58.2	63.2	~37	54.2	Dalla Vecchia (2009)
<i>Bergamodactylus</i> <i>wildi</i> MPUM 6009	-	~15.5	26.3	36	10.5	37.5	~33	36.2	18.5	-	Dalla Vecchia (2009) / AWAK

TABLE II

Ratios of long bone lengths of some Triassic pterosaurs based on the measurements presented in Table I. Some ratios are estimated (~). See text for abbreviations.

Bones/Taxa	sca/ cor	hu/ ul	hu/ mcIV	hu/ ph1d4	ul/ mcIV	ul/ ph1d4	ph1d4/ mcIV	ph2d4/ ph1d4	ph3d4/ ph1d4	ph3d4/ ph2d4	Author
<i>Arcticodactylus</i> <i>cromptonellus</i> MGUH VP 3393	1.93~	0.91	2.17	~1.01	2.39	1.12	~2.14	~1.14	~1.14	~1.00	Jenkins et al. (2001)
<i>Austriadraco</i> <i>dallavecchiai</i> BSP 1994 I 51	1.62	-	-	0.74 (r)	-	-	-	-	-	-	Wellnhofer (2003) / AWAK
<i>Eudimorphodon</i> <i>ranzii</i> MCSNB 2888	-	0.72	1.62	-	2.24	-	-	-	-	-	Wild (1978)
<i>Carniadactylus</i> <i>rosenfeldi</i> MFSN 1797	-	0.76	1.93	0.65	2.62	0.85	3.05	0.91	0.98	1.09	Dalla Vecchia (2009)
<i>Bergamodactylus</i> <i>wildi</i> MPUM 6009	-	0.73	2.50	0.70	3.43	0.96	3.57	0.88	~0.96	~1.10	Dalla Vecchia (2009) / AWAK

Bones/Taxa	ph1d4/ fe	ph1d4/ ti	hu/ fe	hu/ ti	ul/ fe	ul/ ti	fe/ ti	fe/ mcIV	ti/ mcIV	Author
<i>Arcticodactylus</i> <i>cromptonellus</i> MGUH VP 3393	0.91	~0.88	0.92	~0.89	1.02	~0.98	~0.96	~2.35	~2.44	Jenkins et al. (2001)
<i>Austriadraco</i> <i>dallavecchiai</i> BSP 1994 I 51	-	0.92	-	0.68 (r) 0.69 (l)	-	-	-	-	-	Wellnhofer (2003) / AWAK
<i>Eudimorphodon ranzii</i> MCSNB 2888	-	-	1.14	-	1.58	-	-	1.41	-	Wild (1978)
<i>Carniadactylus</i> <i>rosenfeldi</i> MFSN 1797	1.73	1.18	1.13	0.77	1.49	1.02	0.68	1.76	2.58	Dalla Vecchia (2009)
<i>Bergamodactylus wildi</i> MPUM 6009	2.03	-	1.42	-	1.95	-	-	1.76	-	Dalla Vecchia (2009) / AWAK

include *Eudimorphodon ranzii* (MCSNB 2888) and *Bergamodactylus wildi* (MPUM 6009). Based on the points raised above, a new genus is erected for this species, *Arcticodactylus cromptonellus* comb. nov.

Lastly, both bones that might be interpreted as the coracoid are much smaller than the scapula. Only *Austriadraco* has a marked difference between the length of the scapula relative to the coracoid and it is possible that the ratio between the length of these elements of the pectoral girdle (e.g., $sca/cor > 1.50$) could turn out to be a synapomorphy uniting *Arcticodactylus* and *Austriadraco* as part of the Austriadraconidae (see below).

Austriadraconidae fam. nov.

ZooBank Life Science Identifier (LSID) -
urn:lsid:zoobank.org:act:5DE10F05-AB45-4B34-B06A-069FDF4045DC

Type genus: *Austriadraco* gen. nov.

Diagnosis: as for the genus.

Austriadraco gen. nov.

ZooBank Life Science Identifier (LSID) -
urn:lsid:zoobank.org:act:120B3003-6DE3-41B4-AF6B-6F242FB2A777

Etymology: Combination of Austria, the country where the type species was found and *draco*, from the Latin, meaning dragon.

Type species: *Austriadraco dallavecchiai*, type by monotypy.

Diagnosis: as for the type and only known species.

Austriadraco dallavecchiai sp. nov.

ZooBank Life Science Identifier (LSID) -
urn:lsid:zoobank.org:act:6E123721-07EA-419C-B755-9981CC7D9209

Etymology: The species name honors Dr. Fabio Marco Dalla Vecchia, for his studies on Triassic pterosaurs.

Holotype: Incomplete and disarticulated skeleton composed of frontal, jugal, both incomplete mandibular rami, isolated teeth, elements of the vertebral column (cervical, dorsal and caudal

vertebrae), ribs, scapulae and coracoids, humeri, first wing phalanx, pelvis, tibia and fibula. This specimen is housed at the Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Germany (BSP 1994 I 51, Fig. 2, Tabs. I, II).

Locality and horizon: Trail to the Reither Spitze, above the Reither Joch-Alm at about 1600 m height, western Karwendel-Gebirge, southeast of Seefeld in Tyrol, Austria; Seefeld Formation (also known as the *Seefelder Schichten*), Late-Norian (Sevatian) (Wellnhofer 2003).

Diagnosis: This species shows the following autapomorphies: frontal with short anterior processes; jugal with small maxillary and nasal processes, and a thin and elongated postorbital process; presence of an external mandibular fenestra; surangular dorsal process low; scapula significantly longer than the coracoid ($sca/cor \sim 1.62$).

The new species can be further distinguished from other non-pterodactyloid pterosaurs by the following combination of characters: broad coracoid with constricted shaft; deep ischipubic plate; comparatively large tibia relative to the humerus ($hu/ti < 0.70$) and to the first wing phalanx ($ph1d4/ti - 0.92$).

Remarks: This specimen (BSP 1994 I 51) was first described by Wellnhofer (2003), who regarded it as *Eudimorphodon* cf. *E. ranzii* due to the presence of multicuspid teeth. This author acknowledged that some proportions of this material were different from the ones of *Eudimorphodon ranzii* and regarded this specimen as ontogenetically immature or a subadult individual. This young ontogenetic status was mainly based on the fact that BSP 1994 I 51 is about 10 to 25% smaller than the holotype of *Eudimorphodon ranzii* (MCSNB 2888).

Shortly after, Dalla Vecchia (2003b) noted that there were many osteological differences between BSP 1994 I 51 and the holotype of *Eudimorphodon ranzii* (MCSNB 2888), and suggested that it represented a distinct species of that genus.

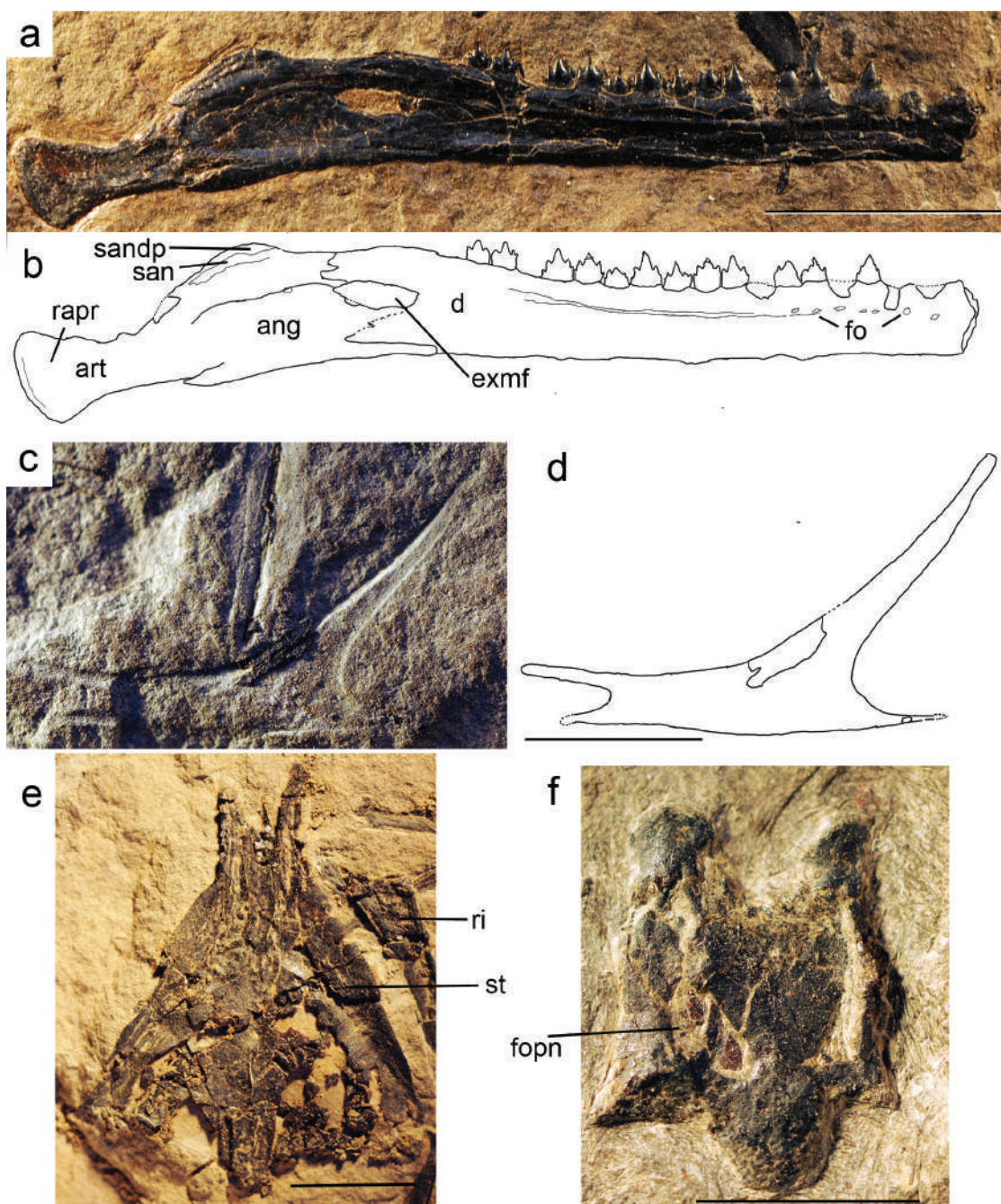


Fig. 2 - *Austriadraco dallavecchiai* (BSP 1994 I 51). (a) Photo and (b) drawing of the right lower jaw. (c) Impression and (d) drawing of the jugal. (e) Sternum. (f) Cervical vertebra from ventral view. See text for abbreviations. Scale bars: (a-b) - 10 mm, (c-f) - 5 mm.

Some years later, Dalla Vecchia (2009) provided several comments on BSP 1994 I 51. He disagreed with Wellnhofer (2003) on the juvenile status of this specimen due to the fusion of several

elements, and was the first to identify (in print) the presence of an external mandibular fenestra. The occurrence of this unusual and important feature was later confirmed by Nesbitt and Hone (2010)

and Bennett (2013, in press). Dalla Vecchia (2009) also provided an extensive phylogenetic analysis of the non-pterodactyloid taxa for all Triassic species and demonstrated that BSP 1994 I 51 was not closely related to *Eudimorphodon ranzii* and might occupy a basal position within the Pterosauria.

The description of Wellnhofer (2003) of BSP 1994 I 51 is very extensive, showing several drawings and illustrations. More recently, Dalla Vecchia (2014) published several colored pictures of this specimen and thus its full description is not necessary here.

This pterosaur skeleton is distributed into five slabs that were collected on different occasions (Wellnhofer 2003). Several bones are preserved as impressions with bits of broken parts, probably due to the exposure of the material prior to collection. Although the skeleton is disarticulated and scattered, there is no duplication of bones and all elements seem to be part of the same individual.

So far, only two cranial elements could be recognized. A flattened bone with two distinct processes was previously identified as a sternum (Wellnhofer 2003, Dalla Vecchia 2014), but is regarded as the fused frontals (pers. observation, Bennett in press). The lack of a cristospine and the developed median ridge that marks the contact between opposite elements corroborate this reinterpretation. The anterior processes of the frontals are shorter than in *Eudimorphodon ranzii*, and apparently also than that of *Bergamodactylus* (MPUM 6009). The notch between them enclosed the posterior processes of the premaxillae.

Except for a small bony portion that forms part of the ventral margin of the orbit and the posterior tip of the quadratojugal process, the jugal is preserved as an impression. It is a tetra radiate element, with the maxillary and nasal processes short and forming a small angle ($\sim 15^\circ$). The postorbital process is thin and long, subequal in length with the ventral margin of this bone, being therefore proportionally

longer than in any other pterosaur. Several thin and flat bones are preserved ventral to the jugal and can be identified as part of the sclerotic ring.

The most interesting element of BSP 1994 I 51 is the lower jaw. As Nesbitt and Hone (2010) pointed out, this bone belongs to the right side and is exposed in lateral view contrary to the original description (Wellnhofer 2003). This interpretation is corroborated by several anatomical observations such as the presence of foraminae and the slightly rugose texture of the bone surface, which is characteristic of the lateral portion of reptilian dentaries.

The mandibular rami are preserved with the right one being more complete and both lacking the symphyseal region. A close examination of the posterior part of the lower jaw did not reveal the presence of a distinct ossification that could be referred to as a 'coronoid' process. Therefore, the observed elevation can be interpreted as a dorsal extension or process of the surangular. This is also true for the holotypes of *Eudimorphodon ranzii* (MCSNB 2888) and *Carniadactylus rosenfeldi* (MFSN 1797), and for MPUM 6009 for which such a structure has been reported (e.g., Wild 1978, Dalla Vecchia 2009, see discussion under *Bergamodactylus*). In any case, the surangular dorsal process is not pointed or developed in BSP 1994 I 51, but rather low and rounded.

The right mandibular ramus clearly shows an external mandibular fenestra, bordered by the dentary, surangular and angular. It has an oval shape and is reduced. The left mandibular ramus is incomplete and also has the anterior margin of an opening that looks like the external mandibular fenestra. However, this opening is significantly larger than the one on the right side. The anterior part of this bone is not preserved but left an impression on the matrix close to the left scapulocoracoid.

The right lower jaw shows 12 multicuspoid teeth in place and two additional alveoli, totalizing 14 teeth. The preserved portion of the left lower

jaw only has the last 10 teeth. There are some differences in the opposite teeth from the left and right side, which were interpreted by Wellnhofer (2003) as ontogenetic or individual variation. The dentary of both sides is shallow compared to other Triassic taxa, similar to that of *Carniadactylus rosenfeldi*. In the preserved portion of the mandible there is a thick anteroposteriorly oriented ridge that is also observed in *Bergamodactylus* (MPUM 6009).

Regarding the postcranial skeleton, it is interesting to mention that one cervical vertebra shows at least one lateral opening in the contact region of the centrum and the neural arch. This opening was correctly interpreted as a pneumatic foramen by Wellnhofer (2003) and is rather rare in the neck of other Triassic pterosaur species (Butler et al. 2009). Pre- and postzygapophyses of the caudal vertebrae are not elongated and do not form rod-like structures. The haemapophyses are long but not to the same degree as in other long-tailed non-pterodactyloid pterosaurs. Scapula and coracoid are fused, with the scapula being a much longer bone. The coracoid is broad and has an expanded proximal end. On the anterior margin of the coracoid a developed ridge runs from the medial opposite portion to the ventral margin of the bone. The articulation of the coracoid with the sternum is dorsoventrally flattened and only slightly concave. The coracoid of BSP 1994 I 51 differs from the more straighter one of *Eudimorphodon ranzii* and shows a more constricted shaft compared to *Carniadactylus rosenfeldi* and MPUM 6009 (which is referred to a new species *Bergamodactylus wildi*, see below). The coracoidal process (= biceps tubercle) is well developed.

Both humeri are preserved, albeit the right one only as an impression. The deltopectoral crest is subrectangular and similar to *Bergamodactylus* (MPUM 6009), but the medial crest is less developed. The left humerus shows a distinct rugose oval depression separated from the remaining part of the deltopectoral crest by a marked diagonal bony ridge. It is not clear if this feature, never

observed in pterosaur humeri before, constitute a taphonomic artifact. No evidence of a pneumatic foramen was observed in both humeri.

The right first wing phalanx is preserved and has the extensor tendon process fused. The pelvis shows the ilium, pubis and ischium fused, being much deeper than in *Eudimorphodon ranzii*. The ischium presents a developed process on the posterior margin. Tibia and fibula are not fused, with the fibula reaching the distal end of the tibia and contacting the proximal tarsals. However, tarsals are fused with the tibia forming a tibiotarsus.

Wellnhofer (2003) considered BSP 1994 I 51 an immature individual mainly due to the slenderness of some bones, including the jugal and the sternum. However, the scapula and coracoid are firmly fused, as is the extensor tendon process of the first wing phalanx, the pelvic bones (ilium, pubis and ischium), and the proximal tarsals with the tibia, suggesting that this specimen represents an adult individual instead.

The marked differences in the anatomy observed in BSP 1994 I 51 justify the establishment of a new taxon, designated here as *Austriadraco dallavecchiai*.

Novialoidea Kellner 2001

Campylognathoididae Kuhn 1967

Bergamodactylus gen. nov.

ZooBank Life Science Identifier (LSID) -
urn:lsid:zoobank.org:act:9EB7F921-85DC-4592-AE9D-658256BDE59F

Etymology: In allusion to the Bergamo Province, in Italy and *dactylus*, from the Greek meaning finger, a common epithet for pterosaur species.

Type species: *Bergamodactylus wildi*, type by monotypy.

Diagnosis: as for the type and only species.

Bergamodactylus wildi sp. nov.

ZooBank Life Science Identifier (LSID) -
urn:lsid:zoobank.org:act:D36DA9AD-FC85-4F85-8882-D8933F7FF1B9



Fig. 3 - *Bergamodactylus wildi* (MPUM 6009), main part of the skeleton. Scale bar: 50 mm.

Etymology: The species name honors Dr. Rupert Wild, who has described several Triassic pterosaurs, including MPUM 6009.

Holotype: An almost complete skeleton housed at the Museo di Paleontologia dell'Università di Milano (MPUM 6009, Figs. 3-4, Tabs. I, II).

Locality and horizon: Cene, Lombardy, Italy; Calcari di Zorzino Formation (Upper Albian) (Dalla Vecchia 2009).

Diagnosis: Campylognathoidid pterosaur that shows the following autapomorphies: gracile postorbital with elongated frontal process;

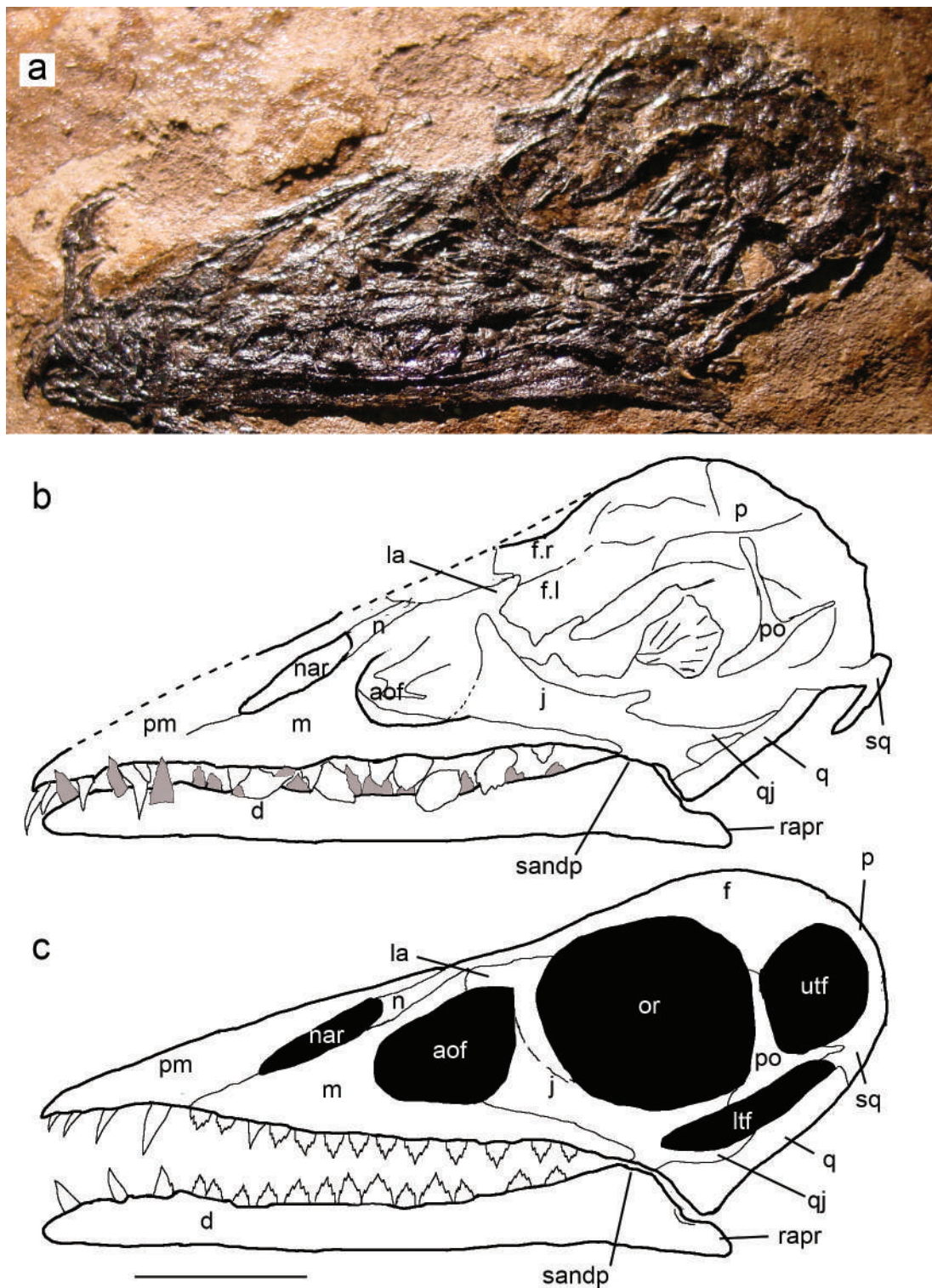


Fig. 4 - The skull of *Bergamodactylus wildi* (MPUM 6009). (a) Photo. (b) Drawing showing the main cranial elements with lower teeth in grey. (c) Reconstruction. Scale bar: 10 mm.

premaxilla not participating in the ventral margin of the external nares; wing metacarpal IV small, about 40% and 30% the length of the humerus and ulna, respectively; femur small, about half the length of the ulna and the first wing phalanx.

The new species can be further distinguished from other campylognathoidids by the following combination of characters: surangular dorsal process of moderate size (smaller than in *Carniadactylus rosenfeldi* but larger than in *Eudimorphodon ranzii*); mandibular rami deeper than in *Carniadactylus*; pteroid rod-like with a marked bend, having the proximal part shorter than in *Carniadactylus*; lack of enlarged maxillary teeth on the middle region of the maxillae (unknown in *Carniadactylus*); dentition of the lower jaw extending more posteriorly than in *Carniadactylus*; 18 and 17 teeth on each side of the upper and lower jaw, respectively.

Remarks: The holotype of *Bergamodactylus wildi* has been described and was illustrated several times in the literature. The first report of MPUM 6009 was done by Wild (1978) in an extensive monograph on the Triassic pterosaurs recovered from Cene (Italy) and most recently by Dalla Vecchia (2014), who presented several colored illustrations of this material.

Wild (1978) nicknamed MPUM 6009 as the 'Milano' specimen' and regarded it as a juvenile of *Eudimorphodon ranzii*. He observed several anatomical differences between this material and the holotype of *Eudimorphodon ranzii* (MCSNB 2888), including dissimilarities in the dentition, but interpreted them as a result of its purported young ontogenetic stage. MPUM 6009 is indeed quite smaller than the holotype of *Eudimorphodon ranzii* with the humerus reaching only about 56% the size of the latter. However, despite this difference, there is no indication that MPUM 6009 is a juvenile. Quite the contrary, size-independent characters commonly used in pterosaur material to assess their ontogenetic stage (e.g., Bennett 1993, Kellner

and Tomida 2000) such as ankylosed scapula and coracoid (as pointed out by Kellner 2003) and the extensor tendon process of the first wing phalanx fused indicate that it represents an adult or "older" subadult animal at time of death. Despite the compressed nature of the specimen, there is also no sign that the carpal elements are unfused, which has also been observed by Dalla Vecchia (2009).

Wild (1978) observed several anatomical differences in the skull and postcranial skeleton of the holotype of *Eudimorphodon ranzii* (MCSNB 2888) and MPUM 6009. This included the shorter skull of MPUM 6009 and a more gracile postorbital, particularly the postorbital frontal process that lacked the dorsal expansion present in the holotype of *Eudimorphodon ranzii* (MCSNB 2888). Furthermore, Wild (1978) recognized that MPUM 6009 had fewer teeth, with 18 in the upper and 17 in the lower jaw, as opposed to 29 and 28 found in the holotype of *Eudimorphodon ranzii* (MCSNB 2888), respectively. He also observed that the enamel of the teeth of MPUM 6009 was smooth, differing from the striated condition present in the teeth of *Eudimorphodon ranzii* (MCSNB 2888).

As pointed out before, there is no indication in MPUM 6009 that suggests that it was a juvenile. Quite the contrary, the fused scapula and coracoid, elements of the syncarpal and the extensor tendon process strongly indicate that this specimen represents an adult individual and therefore the differences registered above cannot be attributed to ontogeny. Although it is conceivable that the skull and lower jaw might indeed get longer in ontogenetically older individuals (e.g., Manzig et al. 2014), there is no example in recent animals that can account for such large variation in number of teeth. In the bone-bed of one pterodactyloid pterosaur from Lower Cretaceous deposits of China, where ontogenetically younger and older individuals were recovered, the number of teeth is constant (Wang et al. 2014). In recent reptiles there might be some changes regarding

the number of teeth due to ontogeny (Edmund 1969), but not as significant as in these pterosaur specimens. Furthermore, MPUM 6009 lacks the two enlarged maxillary teeth below the ascending (or nasal) process of the maxilla which are present in *Eudimorphodon ranzii* (MCSNB 2888). Those teeth were interpreted by Wild (1978) as a result of sexual dimorphism, a hypothesis that cannot be tested on the little number of specimens available.

Another significant difference between MPUM 6009 and *Eudimorphodon ranzii* (MCSNB 2888) is the broad posterior part of the jugal process of the maxillae, which is similar to the condition observed in *Campylognathoides* (e.g., Wellnhofer 1974), but differs from the gently tapering process observed in the holotype of *Eudimorphodon ranzii* (Wild 1978). Moreover, the nasal does not send a thin anterior process to form the dorsoanterior margin of the external nares that is very well developed in MCSNB 2888 (Wild 1978: fig. 25) and might be an autapomorphic feature of *Eudimorphodon ranzii*. The antorbital fenestra of *Eudimorphodon ranzii* (MCSNB 2888) shows the same subtriangular shape than that of MPUM 6009, although being higher, with the dorsal margin surpassing that of the external naris.

Regarding the postcranial skeleton, the main differences observed by Wild (1978) were seen in the pteroid, which is rod-like in MPUM 6009 and lacks the marked proximal expansion observed in the holotype of *Eudimorphodon ranzii* (MCSNB 2888). To my knowledge, no pterosaur species shows such marked differences in the configuration of the pteroid from ontogenetically younger (or smaller) to older (or larger) individuals (e.g., Wellnhofer 1975a, b, c).

Wild (1978) also observed that the humerus of MPUM 6009 is more gracile compared to the one of *Eudimorphodon ranzii* (MCSNB 2888), a difference also regarded as an ontogenetic feature. When both are put in the same scale, the deltopectoral crest of MPUM 6009 extends less down the shaft than in the holotype of *Eudimorphodon ranzii* (MCSNB

2888). Although the variation in the humeri of younger and older pterosaur individuals is still not known in detail, particularly in non-pterodactyloid pterosaurs, a similar change in morphology was observed comparing two humeri of very different sizes of one toothless pterodactyloid species (Manzig et al. 2014), in which one was one third the length of the other. However, when humeri about half the size are compared, there is no difference at all (Manzig et al. 2014: fig. 6a).

In the redescription of '*Eudimorphodon rosenfeldi*', Dalla Vecchia (2009) placed this species into a new genus (*Carniadactylus*) and referred MPUM 6009 to this taxon. Dalla Vecchia (2009) agreed with the observation of Kellner (2003) that MPUM 6009 was not a juvenile, having several bones fused, albeit being much smaller (see comments below). Unfortunately, the holotype of *Carniadactylus rosenfeldi* (MFSN 1797) lacks most of the anterior region of the skull, which limits comparisons.

Among the features used by Dalla Vecchia (2009) to unite MPUM 6009 with *Carniadactylus rosenfeldi*, is the presence of a similar shaped surangular (= 'coronoid') dorsal process (Fig. 5). In any case, a surangular dorsal process is indeed present in *Eudimorphodon ranzii* (MCSNB 2888, albeit located more anteriorly), MPUM 6009 and *Carniadactylus rosenfeldi* (MFSN 1797). Although more developed in the latter, the slope of the posterior margin of the surangular dorsal process in MPUM 6009 and *Carniadactylus rosenfeldi* (MFSN 1797) is more pronounced than in the holotype of *Eudimorphodon ranzii* (MCSNB 2888), a feature shared by those taxa. But, as has been noted by Dalla Vecchia (2009), the dentition in MPUM 6009 does extend posteriorly and is closer to the surangular dorsal process compared to *Carniadactylus rosenfeldi* (MFSN 1797). Since there is no evidence of any tooth in this region in MFSN 1797, this difference does not seem to be an artifact of preservation.

Another difference is observed in the mandibular rami which according to the reconstruction of Dalla Vecchia (2009) is less deep in the holotype of *Carniadactylus rosenfeldi* (MFSN 1797) than in MPUM 6009.

Regarding the postcranial skeleton, Dalla Vecchia (2009) pointed out that the coracoid of MPUM 6009 and *Carniadactylus rosenfeldi* (MFSN 1797) were flat and broad. This author also pointed out the similarities of the pteroid in both specimens that are rod-like and bended. In MPUM 6009 however, the proximal part before the bend is proportionally shorter.

There are also differences in the humerus, with *Carniadactylus rosenfeldi* (MFSN 1797) having the deltopectoral crest comparatively less extended down the humerus shaft. This is not expected in individuals of similar ontogenetic stages (see Manzig et al. 2014 and discussion above).

The proportions of the lengths of several postcranial elements (Tabs. I, II), with the ratios of MPUM 6009 substantially different from the holotype of *Carniadactylus rosenfeldi* (MFSN 1797) and being actually more similar to *Raeticodactylus* (see tables in Dalla Vecchia 2009), also strike as being quite distinct between these two specimens. Overall, the femur in MPUM 6009 is much smaller relative to the humerus, ulna and the first wing phalanx. The same is true for the metacarpal, which is also proportionally shorter relative to several bones in MPUM 6009 compared to other Triassic pterosaurs, including the holotype of *Carniadactylus rosenfeldi* (MFSN 1797). Although in MPUM 6009 and MFSN 1797 the length of the phalanges of the wing finger follow a unique pattern among Triassic pterosaurs, with $ph1d4 > ph3d4 > ph2d4$, proportions between individual phalanges do not reveal any particular pattern. Most interestingly, $ph1d4$ is larger than $ph2d4$, which is rather derived within pterosaurs (e.g., Kellner 2003), but differs from many Triassic and Jurassic species in which these bones are either of the same size or $ph2d4$ is slightly larger. The ratio between $ph3d4$ and $ph1d4$

of both specimens also differ from most other Triassic and Jurassic taxa, where $ph3d4$ is larger than $ph1d4$.

As pointed out by Dalla Vecchia (2009), MFSN 1797 has several bones fused, like the scapula and coracoid, the proximal carpal elements, and the extensor tendon process of the first wing phalanx. Fibula and tibia might also be fused. The sole potential indications that the individual represented by MFSN 1797 might not have reached a full ontogenetic maturity at time of death lies on the unfused distal syncarpals (formed by three elements, Dalla Vecchia 2009) and the presence of a narrow region with a slightly distinct texture between the proximal tarsals and the tibia, indicating that they might not have completely fused despite being otherwise strongly connected.

Regarding the ontogenetic stage of MPUM 6009, this individual has basically the same fused elements as observed in the holotype of *Carniadactylus rosenfeldi* (MFSN 1797): scapula and coracoid, proximal carpal series and the extensor tendon process of the first wing phalanx. The distal portion of the tibia and tarsal elements are not preserved in MPUM 6009. MPUM 6009 has a developed and ossified sternum that is also the case of MFSN 1797. There is no feature that suggests that both specimens represent individuals of very distinct (if at all) ontogenetic stages (see Discussion). Yet regarding size, the maximized wingspan (*maxws sensu* Kellner et al. 2013) of MPUM 6009 is around 465 mm and therefore considerably smaller than the holotype of *Carniadactylus rosenfeldi* (*maxws* - 770 mm).

The differences in anatomical features and size between the holotype of *Carniadactylus rosenfeldi* (MFSN 1797) and MPUM 6009, combined with the developed ontogenetic stage of the latter, indicate that both specimens are not conspecific. Therefore, the taxon *Bergamodactylus wildi* is erected for MPUM 6009. It should also be noted that *Carniadactylus rosenfeldi* comes from a distinct formation, the Dolomia di Forni Formation, that

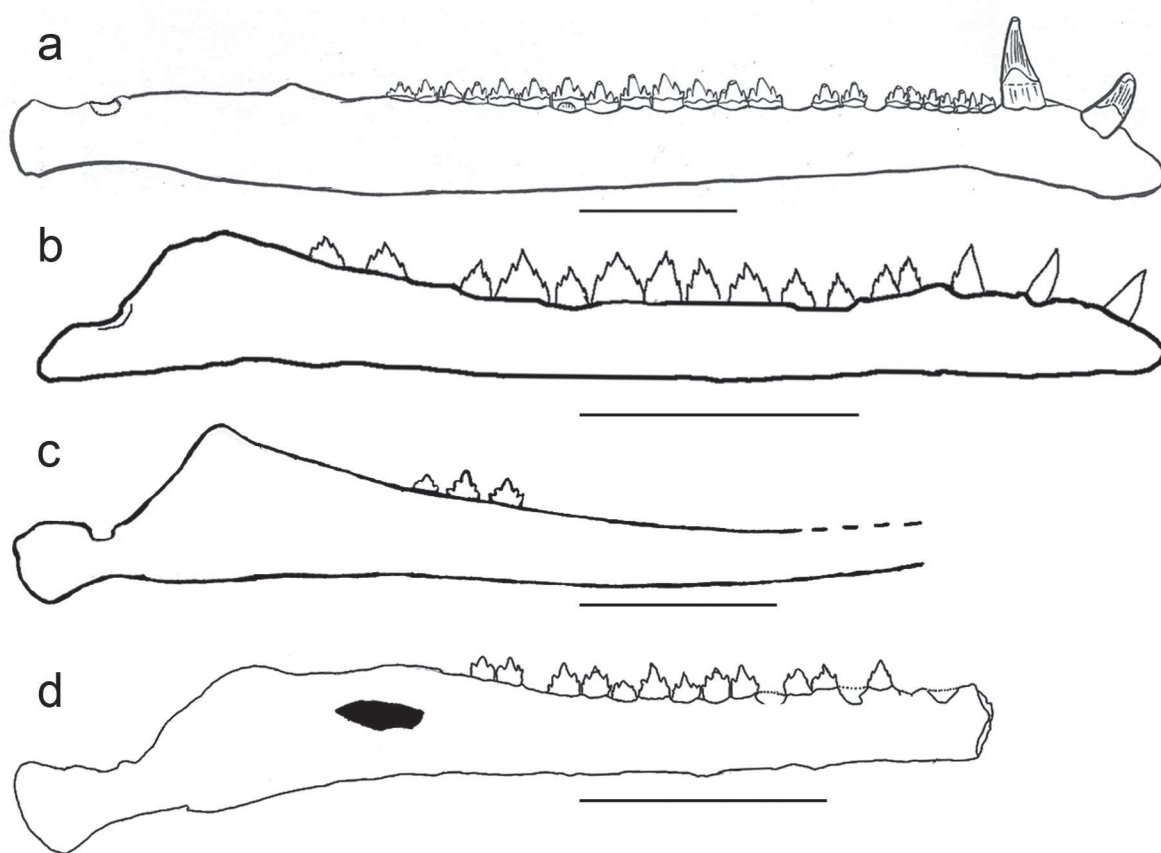


Fig. 5 - Comparison of the lower jaws of Triassic pterosaurs. **(a)** *Eudimorphodon ranzii* (MCSNB 2888, based on Wild 1978). **(b)** *Bergamodactylus wildi* (MPUM 6009). **(c)** *Carniadactylus rosenfeldi* (MFSN 1797, based on Dalla Vecchia 2009). **(d)** *Austriadraco dallavecchiai* (BSP 1994 I 51). Scale bars: 10 mm.

outcrops in the Friuli region and is slightly older than the Calcarei di Zorzino Formation (see Dalla Vecchia 2003a: fig. 1).

DISCUSSION

An adequate evaluation of the anatomical differences concerning taxonomy is a difficult challenge. Besides the usual variation in anatomy due to intrinsic characteristics of organisms (e.g., individual variations, ontogeny, sexual dimorphism, pathology) and ecological factors (e.g., availability of food, climate), fossils have another fundamental set of processes influencing morphology that are imposed by taphonomy. The nature of the fossil record that dictates a general low number of specimens preserved in different grades

of incompleteness, further introduces distortions of variable effects and causes. As expected, these circumstances have influenced pterosaur taxonomy (see comments in Kellner 2010).

Apart from taphonomic biases, which should always be taken into account among the several factors that affect anatomy, one of the recurrent concerns for paleontologists is how to distinguish anatomical differences resulting from ontogeny from those that show taxonomic value. This aspect has been a conspicuous source of debate regarding the taxonomy of Triassic pterosaurs (e.g., Wild 1978, Kellner 2003, Wellnhofer 2003, Dalla Vecchia 2003a, 2009). There are only a few ontogenetic studies addressing the Pterosauria (e.g., Wellnhofer 1975a, b, c, Bennett 1993, 1995,

Kellner and Tomida 2000, Wang et al. 2014, Manzig et al. 2014), which are hampered by the lack of populations than can be confidently assigned to the same species (Kellner et al. 2013). To make matters more complicated, pterosaur anatomy is so distinctive that controversy arises on how modern analogs can be used to shed more light on the ontogeny of those volant reptiles (e.g., Wild 1978, Padian 1983, Sayão 2003, Chinsamy et al. 2008).

In any case, fusion of bones has been regarded as one effective way to determine ontogenetic stages among pterosaurs. The problem, however, is that most distinctions are limited to three categories: juveniles, subadults and adults. Although the extremes are easily recognized, ontogenetic variation of subadults and even the distinctions of 'old subadults' from adults have proved to be difficult and controversial. Furthermore, the category of subadults has been applied rather loosely and therefore revealed to have little utility in pterosaur taxonomy.

Although some authors have tried to provide a general notion of which bones tend to fuse earlier than others (e.g., Kellner and Tomida 2000), there is a general lack of refinement regarding the ontogenetic fusion sequence in pterosaurs. Aware of the complexity related with this issue that includes the likelihood of species and groups of species developing distinct ontogenetic paths, here I show a preliminary attempt to provide an ontogenetic refinement within the Pterosauria that might also be applicable at least to their closer relatives.

It has been observed that several bones or complex of bones tend to fuse in adult pterosaur specimens. Regarding the skull, there is a tendency of most elements to fuse completely during ontogeny somehow similar to what happens in birds, but perhaps at a slower pace. The same is true for the lower jaw, where the suture of the posterior bones (e.g., angular, surangular) are closed in ontogenetically more developed individuals.

Concerning the postcranial skeleton, the following elements have been observed to fuse in pterosaurs: vertebral centrum and neural arches, dorsal vertebrae forming a notarium (with a distinct number of elements), sacral vertebrae (also with a different number of elements), scapula and coracoid, two epiphyses at the distal portion of the humerus, one epiphyseal plate at the proximal articulation of the ulna, the elements of the proximal carpals series (two), the elements of the distal carpal series (up to four), the extensor tendon process of the first wing phalanx, pelvic elements (ilium, pubis and ischium), opposite prepubia, pelvic elements with the sacrum, fibula with tibia, proximal tarsals (calcaneum and astragalus), and the proximal tarsals with tibia (forming a tibiotarsus). Based on several observations of the fusion of these bones done on non-pterodactyloids (e.g., Wellnhofer 1975a, b, c, Bennett 1995, Dalla Vecchia 2003a, 2009, Wang et al. 2010) and pterodactyloids (e.g., Bennett 1993, 1996, Kellner and Tomida 2000), a preliminary classification of six ontogenetic states (OS) is proposed and discussed below. It should be noted that the current knowledge on growth variation within the Pterosauria does not allow the establishment of a complete sequence of all postcranial elements that fuse during growth.

OS1 - all bones or complex of bones unfused, ossification of some elements like the sternum and the articulations of some long bones (ulna, radius, wing phalanges, tibia) present, but not fully developed. This is the condition of hatchlings.

OS2 - all bones ossified although the degree of ossification might vary, with all long bones having their articular ends molded. The texture of the external bone surface is immature, showing pits and small struts of bones. OS2 represents the condition of juveniles. It should be noted that in most derived pterosaurs and in some non-pterodactyloids, the dentaries (and likely all cranial elements) are also unfused. However, in some non-pterodactyloids, the dentaries do not fuse even in adult individuals such

as in the holotype of *Eudimorphodon ranzii*. In this respect, the fusion of the dentaries show both, an ontogenetic condition (for most pterosaurs) and also a phylogenetic signal (for some non-pterodactyls), although the latter needs further investigation.

OS3 - fused sacral vertebrae, followed by fusion of the carpal elements, with the distal carpal elements fusing earlier than the ones of the proximal series.

OS4 - scapula and coracoid are fused, followed by the pubis and ischium that form a puboischiadic plate. The ilium, however, is not fused with the remaining elements of the pelvic girdle at this ontogenetic stage.

OS5 - ilium fused with the puboischiadic plate and the extensor tendon process fused with the wing phalanx.

OS6- all bones or complex of bones are fused. The epiphyses of the humerus are among the last bones to fuse, with the larger distal epiphyseal plate fusing before the smaller ventrodistal epiphysis. Furthermore, the epiphyseal plate of the proximal articulation of the ulna is among the last bones to fuse. At this stage, ontogenetic maturity has been reached and specimens can be considered full adults from the ontogenetic point of view.

It should be noted that even when pterosaurs reach OS6, this does not mean that ossification stops. One specimen of an anhanguerid pterodactylid (Kellner et al. 2013) has all bones fused and histological thin sections show a developed external fundamental system suggesting that growth had essentially ceased or was occurring at a very low rate when this animal died. However, the neural spines of some dorsal vertebrae that form the notarium were still in the process of being totally connected.

In several pterosaurs (non-pterodactyls and pterodactyls alike) opposite puboischiadic plates fuse and form a ventral pelvic symphysis. It is not clear if the lack of this fusion could be related to sexual dimorphism since an open pelvic symphysis at the ventral portion would allow some aperture of the pelvis during oviposition.

Considering the classification above, the holotype of *Arcticodactylus cromptonellus* (MGUH VP 3393) and *Eudimorphodon ranzii* (MCSNB 2888) represent ontogenetic extremes, OS2 and OS6, respectively. Nevertheless, the anatomical differences are substantial and Jenkins et al. (2001) were correct in raising a new species for MGUH VP 3393, a decision that had not been questioned in the literature and therefore will not be further discussed here.

The holotype of *Carniadactylus rosenfeldi* (MFSN 1797) also has several bones fused, including the extensor tendon process of the first wing phalanx and therefore has reached at least OS5. It is not easy to be sure if the epiphyseal bones of ulna and humerus are also fused, the main reason precluding the assignment of MFSN 1797 to OS6. In addition, the proximal tarsals are not completely fused with the tibia, although the fusion process had already taken place (Dalla Vecchia 2009).

Based on the same reasons, the holotypes of *Bergamodactylus wildi* (MPUM 6009) and *Austriadraco dallavecchiai* (BSP 1994 I 51) have also reached at least OS5, which is supported particularly by the fused extensor tendon process. Moreover, BSP 1994 I 51 has the ilium fused to the puboischiadic plate (not visible in MPUM 6009), which is here regarded as another indicator of this ontogenetic stage.

The holotypes of *Carniadactylus rosenfeldi* (MFSN 1797), *Austriadraco dallavecchiai* (BSP 1994 I 51) and *Bergamodactylus wildi* (MPUM 6009) clearly represent individuals of the same or very similar ontogenetic age. Therefore, the several anatomical differences cannot be considered as a result of ontogeny.

Concerning BSP 1994 I 51, there seems little doubt that this specimen represents a new species (e.g., Dalla Vecchia 2009), but the taxonomic status of MPUM 6009 is more problematic. Wild (1978) and Dalla Vecchia (2009) have each referred this specimen to distinct previously known species.

As has been pointed out, Wild (1978) regarded all differences between MPUM 6009 and holotype of *Eudimorphodon ranzii* (MCSNB 2888) as ontogenetic, which is dismissed here and was also rejected, at least in part, by some authors (e.g., Kellner 2003, Dalla Vecchia 2009).

Although concluding that MPUM 6009 was not a "very immature individual", Dalla Vecchia (2009) regarded this specimen to represent *Carniadactylus rosenfeldi*. Indeed, there are some anatomical similarities between MPUM 6009 and the holotype of *Carniadactylus rosenfeldi* (MFSN 1797), as has been acknowledged here, but there are also significant differences, some observed by Dalla Vecchia (2009) as well. Among the most conspicuous one, is the position of the last tooth of the lower jaw, more posterior located in MPUM 6009. Dalla Vecchia (2009) suspected that this difference might be taphonomic, a hypothesis to which I have found no support during close examination of MFSN 1797.

Other differences include the proportions of bones that were dismissed as possible individual variations (Dalla Vecchia 2009). However, some of the bone ratios are quite distinct, such as the ratio of the wing metacarpal IV relative to the humerus and to the ulna, and the ratios of the femur relative to the ulna and to the first wing phalanx. If these differences are due to individual variation then perhaps the ratios of bones might not show any taxonomic signal at all, a view that is not advocated here.

Furthermore, the significant size difference between these two specimens of the same ontogenetic stage must be emphasized, with the maximized wingspan of MPUM 6009 being around 60% the maxws of the holotype of *Carniadactylus rosenfeldi* (MFSN 1797). Theoretically, it might be possible that MFSN 1797 was a giant or that MPUM 6009 was a dwarf of a same species that lived (or died) in distinct islands during the Triassic times (as paleogeographic reconstructions have shown, see Dalla Vecchia 2014). However, in my opinion,

the anatomical differences argue against these interpretations. The holotype of *Bergamodactylus wildi* (MPUM 6009) has two of the main qualities to be recognized as a new species (see Kellner 2010): differences in anatomy and provenance from a distinct stratigraphic layer.

There has been an interesting discussion in the literature regarding the so-called 'typological' versus 'realistic' approach to taxonomy of fossils (e.g., Bennett 1996), in which the main question resides on how anatomical differences should be evaluated. The key arguments for the 'realistic' approach is the fact that in nature several anatomical variations are observed in recent populations and they should be expected to be found in the fossil record as well. Granted that this could be the case, in my opinion the only way that one could confidently address this issue is having specimens that make part of the same or at least similar populations at hand. This can only happen with the discovery of bone-beds with complete (or nearly complete) material. So far, only three of such pterosaur accumulations have been discovered (Chiappe et al. 1998, Wang et al. 2014, Manzig et al. 2014), and the development of specific studies on this material (e.g., paleohistology, detailed ontogenetic analyses) might provide an opportunity to better address this issue.

Lastly, a fragment of a lower jaw that was tentatively referred to *Eudimorphodon* might represent the oldest pterosaur known so far and is currently under study (Andres and Myers 2013). By examining the published pictures of this material (Murry 1986: figs. 9.5H) it is unlikely that this specimen could be conclusively referred to this genus and probable represents a new taxon, further increasing the Triassic pterosaur diversity.

CONCLUSION

Some specimens assigned to the genus *Eudimorphon* and to the species *Eudimorphodon ranzii* have been reviewed, and based on significant anatomical differences assigned to new taxa: *Arcticodactylus*

cromptonellus (comb. nov.), *Austriadraco dallavecchiai* (gen. et sp. nov.) and *Bergamodactylus wildi* (gen. et sp. nov.). An analysis of pterosaur ontogeny leads to the recognition of distinct ontogenetic stages (OS), leading to the definition of six classes (OS1-OS6). Based on these, the holotype of *Arcticodactylus cromptonellus* (MGUH VP 3393) belongs to OS2, but the conspicuous anatomical differences distinguishes it from all other basal pterosaurs. The holotypes of *Austriadraco dallavecchiai* (BSP 1994 I 51) and *Bergamodactylus wildi* (MPUM 6009) represent individuals that have reached at least OS5, the same ontogenetic stage as the holotype of *Carniadactylus rosenfeldi* (MFSN 1797), and therefore the anatomical differences observed between them cannot be explained by ontogeny. In addition, *Bergamodactylus wildi* is significantly smaller than *Carniadactylus rosenfeldi* with the maxws of the holotype (MPUM 6009) around 60% that of *Carniadactylus rosenfeldi* (MFSN 1797). Although it is hypothetically possible that these specimens found in distinct islands of the Triassic and of equal ontogenetic stages might represent extremes of growth of the same species (sexual dimorphisms being excluded), the significant anatomical differences, which include substantial variation in the proportions of some bones, argue against this interpretation and suggest that they belong to distinct species. Granted that more specimens and a better refinement of ontogenetic age based on osteological maturity is paramount to better understand the significance of anatomical differences within the Pterosauria, the results presented here show that the diversity of those volant reptiles in the Late Triassic is greater than previously thought, pushing the origins of this clade back to at least to the Middle Triassic.

ACKNOWLEDGMENTS

I wish to thank the following curators for allowing access to specimens under their care: Anna Paganoni (Museo Civico di Scienze Naturali di Bergamo,

Bergamo - 1994, 2001 and 2003), Giuseppe Muscio (Museo Friulano di Storia Naturale, Udine - 1994, 2001 and 2003), Andrea Tintori (Museo di Paleontologia dell'Università di Milano, Milan - 1994, 2001 and 2003) and Oliver Rauhut (Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich - 2003, 2007 and 2014). I also thank Taissa Rodrigues for providing pictures of *Arcticodactylus cromptonellus* and Xin Cheng for sharing some of his research on wukongopterids. I would also like to acknowledge five reviewers for providing several suggestions that greatly improved this paper. Lastly, I express my gratitude to Fabio M. Dalla Vecchia and Rupert Wild for many productive and stimulating discussions about pterosaurs, particularly those from Triassic deposits. This project was partially supported by the Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ # E-26/102.737/2012) and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq # 304780/2013-8).

RESUMO

Eudimorphodon ranzii foi o primeiro pterossauro descrito do Triássico e, baseado na ocorrência de dentes multicuspidados, diversos exemplares foram referidos a esse táxon. Uma vez que essa característica dentária foi observada em diversos outros pterossauros, a revisão de alguns espécimes referidos a *Eudimorphodon* revelou que estes representam os seguintes novos táxons: *Arcticodactylus cromptonellus* (comb. nov.), *Austriadraco dallavecchiai* (gen. et sp. nov.) e *Bergamodactylus wildi* (gen. et sp. nov.). Uma análise preliminar da ontogenia de pterossauros levou a identificação de seis classes ontogenéticas (OS1-6). De acordo com essa classificação, o holótipo de *Arcticodactylus cromptonellus* atingiu o estágio OS2. Mesmo levando em conta a marcada diferença ontogenética entre esse espécime e os demais, as diferenças anatômicas o excluem de *Eudimorphodon*. Os holótipos de *Austriadraco dallavecchiai* Berga-

modactylus wildi e *Carniadactylus rosenfeldi* atingiram ao menos o estágio OS5, demonstrando que as diferenças anatômicas observadas não podem ser explicadas pela ontogenia. Ademais, *Bergamodactylus wildi* atinge aproximadamente 60% da abertura alar maximizada de *Carniadactylus rosenfeldi* e corrobora com a noção de que essas espécies encontradas em distintas ilhas existentes durante o Triássico não eram conspecíficas. O presente estudo aumenta a diversidade de pterossauros triássicos e indica que a origem do clado teria ocorrido no Triássico Médio.

Palavras-chave: Pterosauria, Ontogenia, *Eudimorphodon*, *Arcticodactylus*, *Austriadraco*, *Bergamodactylus*.

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